



USING FIRE HISTORY MODELS TO ESTIMATE PROPORTIONS OF OLD GROWTH FOREST IN NORTHWEST MONTANA, USA

Peter Lesica

Conservation Biology Research, 929 Locust, Missoula, Montana 59802, USA and Division of Biological Sciences, University of Montana, Missoula, Montana 59812, USA

(Received 17 October 1994; accepted 26 September 1995)

Abstract

Mature and post-mature stands may be under-represented in many modern forest landscapes as a result of preferential harvest of these age classes. It is important for land managers concerned with protecting biological diversity to know the approximate proportion of old growth in forest landscapes prior to European interference. Negative exponential models, based on mean standreplacing fire intervals taken from fire history studies, were used to estimate presettlement stand-age distributions for three areas in northwest Montana. Results were compared with empirical distributions calculated from stand maps prepared in 1937-38, prior to significant timber harvest and effective fire suppression. The models predicted the observed proportion of 1937-38 old growth (≥200 years) within 10% but were poor at predicting proportions in 20-year age classes. These results suggest that negative exponential models based on empirically determined estimates of fire interval can be used to obtain approximate estimates of presettlement old growth if local fire history studies have been done. Results of this study and numerous fire-history studies suggest that old growth occupied 20-50% of many presettlement forest ecosystems in the Northern Rockies. Copyright © 1996 Elsevier Science Ltd

Keywords: Montana, old growth, fire history models, forest conservation.

INTRODUCTION

One goal of modern forestry is to use ecological principles to manage forest lands for both commodity production and the conservation of species diversity (Norse et al., 1986; Hansen et al., 1991). In order to attain this goal it is necessary to have forests with all successional stages in quantities and spatial arrays like those to which resident organisms are adapted (Harris, 1984; Bunnell, 1995). During the past decade attention 1 western North America has been focused on mature

Correspondence to: P. Lesica, Tel.: 406-728-8740; Fax: 406-243-4184.

and especially post-mature (i.e. old growth) forests (Morrison, 1988; Norse, 1990). Conservation advocates believe that the extent of old growth forests has been reduced by harvest activities to the point where many species are jeopardized. However, land management agencies and private timber interests often argue that the present inventory of old growth is similar to presettlement levels, and conservation is unnecessary (USDA Forest Service, 1992).

Unfortunately, knowledge of forest age structure prior to European disturbance is often difficult to obtain. In some cases this information can be obtained from historical documentation. However, quantifiable historical information is not available for many areas of western North America. In these cases a method for estimating the proportion of old forests on the presettlement landscape would be useful to those managing land for biological diversity.

Historically, fire has been an integral part of forest ecosystems in the Northern Rocky Mountains and was certainly the most important disturbance structuring these systems prior to European settlement (Wellner, 1970; Arno, 1980; Habeck & Mutch, 1983). Fire regime was the principal factor determining the mosaic of different stand ages across the landscape. At low elevations, drier habitats experienced frequent non-lethal fires, while moist sites were more likely to have had infrequent stand-replacing fires. At higher elevations, cool slopes experienced infrequent lethal fires, while warmer slopes experienced a mixture of more frequent stand-replacing and non-lethal fires (Barrett & Arno, 1991). Forest habitats with infrequent stand-replacing fires would have supported greater proportions of mature and old-growth forests.

There have been several attempts to model the relationship between fire interval and age-class distribution mathematically. Van Wagner (1978) proposed the negative exponential distribution as an approximation to this relationship. The Weibull model takes changing flammability with stand age into account and has been considered by some to be more ecologically realistic (Johnson, 1979; Yarie, 1981). These models have been shown to fit fire frequency data collected in coniferous

34 P. Lesica

forests from a variety of landscapes throughout boreal and cordilleran western North America. Although Johnson (1979) found that the Weibull model better described fire behavior in northwest Canada, he also showed that the Weibull model was nearly equivalent to the negative exponential model when terrain was broken, suggesting that the negative exponential model is appropriate for the Northern Rocky Mountains.

Rowe et al. (1975) found that the Weibull model fit their data from northwest Canada better than the negative exponential model. However, McCune (1983) and Johnson and Larsen (1991), working in the more mountainous terrain of western Montana and west-central Alberta respectively, determined that the negative exponential model fit their data well, and Yarie (1981) found that the two models fit most of his data from Alaska equally well. The majority of studies from similar landscapes suggest the negative exponential model provides a good approximation for fire behavior in mesic forests of the Northern Rocky Mountains. Maximum likelihood estimates for negative exponential and Weibull distributions for my data were very similar.

Even though they make many simplifying assumptions, Van Wagner (1978) proposed that negative exponential models can be used to estimate presettlement stand-age distribution as well as the expected proportion of forest in particular age classes given mean stand-replacing fire interval and that certain assumptions are met. Thus, a simple equation relates the proportion of old forests to the mean stand-replacing fire interval. However, Baker (1989) argued that estimates of mean fire frequency cannot be used to this end because fire intervals are too variable.

The purpose of this study is to use empirical estimates of stand-replacing fire intervals to test predictions of proportions of old growth (defined solely on the basis of age) derived from simple fire history models. This comparison can be made in northwest Montana because both historical data and estimates of pre-interference fire frequency are available. The US Forest Service conducted timber inventories of forested lands in western Montana from 1937 to 1943. These inventories can be used to determine the distribution of stand ages at a time before significant timber harvest and effective fire suppression. Fire history studies have been conducted in western Montana, and estimates of mean stand-replacing fire intervals are available for some areas (Arno, 1980).

MATERIALS AND METHODS

Study areas

Each study area consisted of six townships (56,000 ha) and was adjacent to or included the site of a previous study that provided an estimate of mean stand-replacing fire interval (Fig. 1). Forests with similar site potential, successional patterns and fire disturbance regimes are called 'fire groups' (Fischer & Clayton, 1983;

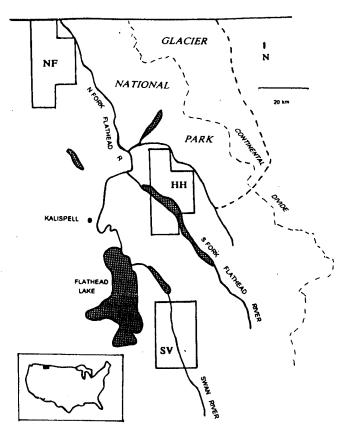


Fig. 1. Location of study sites in northwest Montana: (HH) Hungry Horse, (NF) North Fork, (SV) Swan Valley.

Fischer & Bradley, 1987) and were assigned according to Fischer and Bradley (1987). Only stands classified to the dominant fire group for that study area were included in the analyses.

Hungry Horse

The moist lower subalpine fire group is dominant with Abies lasiocarpa as the climax species in most stands, and Larix occidentalis, Pinus contorta and Pseudotsuga menziesii as the most common seral species. The analysis area was 18,515 ha, and 1065–1890 m elevation. Mean stand-replacing fire interval before 1910 at the north end of the study area was 121 years below 1650 m (Davis, 1980).

North Fork

Dominant fire group and species composition are similar to those at Hungry Horse. Analysis area was 28,090 ha and 1220–1890 m in elevation. Barrett et al. (1991) conducted a fire history study along the North Fork of the Flathead River in Glacier National Park 1 km east of this area and estimated mean stand-replacing fire interval to be 186 years prior to 1935.

Swan Valley

The moist grand fir/western redcedar fire group domin. the valley floor at 975-1400 m with *Abies grandis* and *Thuja plicata* as the climax species, and *Larix occidentalis*,

Pinus monticola and Pseudotsuga menziesii the most common seral species. The analysis area was 19,750 ha. A study of this fire group in the Middle Fork of the Flathead River drainage in Glacier National Park 90 km to the north estimated the mean stand-replacing fire interval prior to 1935 to be 261 years for this fire group (Barrett et al., 1991).

Fire history models

In the negative exponential model the proportion of stands reaching a particular age is the random variable, and the reciprocal of mean fire interval (probability of fire in a stand) is the only parameter. A lucid discussion of the model's derivation is presented by Van Wagner (1978). The cumulative proportion of all stands less than or equal to age t is given by

$$F(t) = 1 - \exp(-pt) = 1 - \exp(-t/b) \tag{1}$$

where p is the annual probability of fire in any one stand and b = 1/p is the mean fire interval (Van Wagner, 1978). For example, the % of stands 101-120 years old is

Stands₁₀₁₋₁₂₀ =
$$[\exp(-101/b) - \exp(-120/b)] \times 100$$
 (2)

This model assumes that stand flammability is constant with age. If fire hazard increases with stand age, then the model will overestimate the proportion of very old stands (Van Wagner, 1978).

In order to use mean fire interval models to estimate average presettlement stand-age distribution, the following assumptions must be met:

- (1) Mean fire interval is determined on a point or stand basis (Hawkes, 1980; Arno & Petersen, 1983).
- (2) Estimates of mean fire interval apply only to areas with similar fire regimes, topography and histories of human-caused fires (Hawkes, 1980; Johnson & Van Wagner, 1985).
- (3) Mean fire interval must be determined from the time predating effective fire suppression.
- (4) The size of the study area must be large compared to the extent of the largest fire (Johnson & Van Wagner, 1985; Baker, 1989). Johnson and Gutsell (1994) propose the general rule that study areas in which $\geq 33\%$ of the area has been burned by a single fire are too small. Fire history models provide an estimate of proportion of stands in each age class. In order to compare the predictions of the models with the observed areal data and to estimate the proportion of forested landscape in old-growth condition, it is necessary to assume that the proportions of stands and area are equivalent (W. Baker, pers. comm.), i.e. the size distributions within the different age classes must be similar. This assumption becomes more reasonable as the number of stands in each class becomes larger. Thus, larger study areas and/or broader age classes will yield more robust results.

With one exception, my study met the assumptions of the fire history models. Fire interval was determined

by examining fire scars and cohort regeneration on a stand basis and preparing master fire chronologies (Davis, 1980; Barrett et al., 1991). Only stands with similar fire regimes (i.e. in the same fire group) were used in the analysis, Estimates of mean stand-replacing fire interval were made before fire suppression became effective (Arno & Sneck, 1977; Pyne, 1982). Fires, or perhaps a single fire, occurring in the 1920s initiated 31% of the stands in the Hungry Horse study area (Fig. 2), suggesting that the study area may have been too small (Johnson & Gutsell, 1994). Otherwise no single 20-year interval accounted for initiation of more than 16% of the stands in any study area (Fig. 2). Every township in the study had stands of numerous different ages. Thus, it is reasonable to assume that the size of the study areas was sufficiently large.

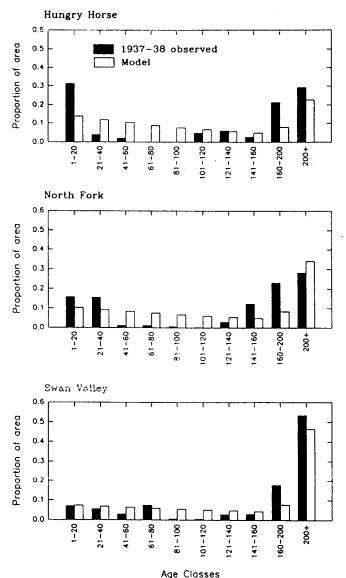


Fig. 2. Age class distribution of forest stands for three study areas in northwest Montana determined from (1) 1937-38 stand exam maps (filled bars) and (2) mean fire frequency models (open bars). Distributions appear bimodal or skewed to the left rather than skewed to the right because the two oldest age classes encompass more than 20 years.

36 P. Lesica

Historical data

I compared results derived from negative exponential models with empirical data from stand maps prepared in 1937–38. Age of the cohort having the greatest basal area was determined from increment cores taken by surveyors. Stand boundaries were delineated on the ground, with the aid of aerial photography (Hart & Lesica, 1994). Stands were placed in 20-year age classes up to 160 years and then 160–200 years and 200+years. Forests above 2130 m were generally considered non-commercial and were not examined. Stands were delineated on 1:31,700 maps (USFS, 1937–43).

Hart and Lesica (1994) assessed the degree of congruency between these early age estimates and those from stand exams made during the last decade. They found that 52% of the early estimates were within 20 years of the modern estimates, and less than 27% showed discrepancies of greater than 60 years. There was no bias toward either older or younger estimates. and the distribution of discrepancies was symmetric about zero. Thus, when a large number of stands are considered, the distribution of age classes should be reasonably accurate. Discrepancies may be the result of errors in either the early or modern exams or differences in how stand age was determined for the two data sets. Although far from perfect, these early maps provide the best one-point-in-time estimates of stand age distribution previous to timber harvest and fire suppression available for western Montana.

For each study area the dominant fire group was used to obtain the estimate of mean stand-replacing fire interval. All stands in that fire group were located using 1:24,000 stand maps based on surveys conducted by the US Forest Service, Montana Department of State Lands and Plum Creek. Thus, the fire regime of the lands I mapped was similar to that on which the fire frequency estimate was based. Areas were calculated for each age class using 1:2.4 ha dot grids.

RESULTS

Stand-age distributions, using 20-year classes derived from mean fire interval models, were significantly different than from distributions derived from 1937–38 data (Fig. 2; Kolmogorov-Smirnov test, p < 0.01). The models underestimated proportions in the two oldest age classes in five of six cases (Fig. 2).

Although the mean fire interval models predicted individual 20-year age classes poorly for the 1937–38 data, predictions for the 200+ class were relatively accurate (Fig. 2); model predictions of old growth proportions were all within 6–10% of observed proportions.

DISCUSSION

Model performance

There are a number of possible reasons for the models' failure to predict observed distributions. The poor fit is

most likely due to the large variance in the size and frequency of fires compared to the size of the age classes. Fire hazard in the Northern Rocky Mountains is not constant over short periods but can vary on the scr of decades due to prolonged periods of drought cool, wet weather. As a result, some 20-year age classes are large due to extreme fire years, while others are small as a result of long fire-free periods. A model based on a single mean fire interval derived from 300-500 years of fires will not be robust at predicting point-in-time distributions when small age classes are used (Baker, 1989). Estimates of mean stand-replacing fire intervals were taken from study areas close to my study areas, but the lack of exact geographical correspondence could introduce errors into estimates obtained from the fire history models. Estimates of mean fire interval obtained without random sampling of fire-scarred trees may be biased (Johnson & Gutsell, 1994); however, there is no reason to suspect any systematic bias in the data collection (S. Barrett, pers. comm.). In some areas fire cycles have changed in the 200-400 years preceding fire suppression (reviewed in Johnson, 1992). If the change in fire frequency was large, models based on mean fire interval for the whole period could not accurately predict age-class distribution for a single point in time.

The 200+ class encompasses c. 200 years, an order of magnitude larger than the other classes. This is undoubtedly the reason for the increased accuracy of area predictions for this class. Using large age-clas reduces the effect of the variance associated with t size and frequency. Larger study areas would likely have increased the accuracy of the estimates, especially in the Hungry Horse area.

One explanation for the consistent underestimates in old classes is that the negative exponential model assumes a constant hazard of fire, but old stands are less prone to stand-replacing fire than young and moderate-age stands (Van Wagner, 1977). The underestimates may also result from some stand-replacing fires failing to kill all of the trees in the stand, especially fire-resistant species such as western larch (Barrett *et al.*, 1991). If enough larch survived, 1937–38 timber surveyors may occasionally have recorded the survivors as the dominant cohort.

Implications for conservation

Negative exponential fire history models can be useful for estimating approximate proportions of old growth in presettlement forest landscapes where fire is the dominant force controlling stand replacement. In the Northern Rocky Mountains, mean stand-replacing fire frequency is variable even within the same fire group (Table 1; Arno, 1980). Thus, it is important to use localized fire history data to estimate the mean sta replacing fire interval. Such studies can provide magers with information useful for setting guidelines for the conservation of old growth in many forest landscapes.

Table 1. Mean stand-replacing fire intervals and estimated % of presettlement old growth (>200 years old) forest (OG) in different fire groups (Fischer & Bradley, 1987) in the Northern Rocky Mountains of northern Idaho (ID) and western Montana (MT) % old growth was derived using negative exponential models computed from mean fire interval (eqn 2).

Fire group	Location	Elevation (m)	Source	Mean fire interval	OG %
Warm dry Douglas fir	ID	550-1615	Barrett & Arno (1991)	>200	>37
Moist Douglas fir	MT	1100-1575	Barrett et al. (1991)	186	34
Dry lower subalpine	MT	1800-1910	Davis (1980)	>146	>25
Cool lodgepole pine	ID	1615-2285	Barrett & Arno (1991)	117	18
Moist lower subalpine	MT	1000-1140	Davis (1980)	>117	>18
Moist lower subalpine	MT	1200-1650	Davis (1980)	121	19
Moist lower subalpine	MT	1575-1800	Davis (1980)	146	25
Moist lower subalpine	ID	1430-130	Arno & Davis (1980)	>150	>26
Moist lower subalpine	ID	15251980	Barrett & Arno (1991)	174	32
Moist lower subalpine	MT	1200-1575	Barrett et al. (1991)	186	34
Moist lower subalpine	MT	1220-1830	Barrett et al. (1991)	202	3 4 37
Grand fir/cedar-hemlock	MT	1260-1400	McCune (1983)	63	31
Grand fir/cedar-hemlock	ID	760-1525	Arno & Davis (1980)	100	14
Grand fir/cedar-hemlock	ID	1280-1830	Barrett & Arno (1991)	119	14
Grand fir/cedar-hemlock	ID	550-1280	Barrett & Arno (1991)	119	19
Grand fir/cedar-hemlock	ID	760-1065	Arno & Davis (1980)	>200	36
Grand fir/cedar-hemlock	МТ	975–1525	Barrett <i>et al.</i> (1991)	261	>37 46

There is evidence that native vertebrate faunas are adapted to particular fire regimes and stand age distributions (Bunnell, 1995). Furthermore, many species of plants and animals require or find optimum habitat in old-growth forests of the Northern Rocky Mountains (McClelland, 1979; Hejl & Wood, 1991; Lesica et al., 1991). Although old growth is often defined by structural as well as age characteristics (Old Growth Definition Task Force, 1986), stand age is strongly correlated with structural characters as well as the occurrence of many animal species (Franklin et al., 1981; Norse, 1990). Theory and empirical studies predict that many species will have difficulty maintaining genetically and demographically viable populations in a greatly reduced habitat base (Harris, 1984: Gilpin & Soulé, 1986; Wilcove, 1987; Gilpin, 1988; Doak, 1989).

Results of this study and model estimates based on fire history studies throughout the Northern Rocky Mountains (Table 1) suggest that old growth occupied 20–50% of the presettlement forest landscape in low-and many mid-elevation habitats. Yet most national forests in the Northern Rocky Mountains plan to maintain at most 10% of their total forest inventory in old growth (Yanishevsky, 1987). Low-elevation land-scapes have suffered the greatest losses because much of this land is owned by private companies who have harvested all or nearly all of their ancient forests. A reduction from 20–50% to less 10% in old growth in low- to mid-elevation forests may well cause extirpation of many old-growth dependent species.

Fire suppression and management for timber production have greatly altered the age-class distribution of stands on forested landscapes (Arno, 1976; Habeck, 1983; Harris, 1984; McCune, 1983). By reducing the occurrence of low intensity burns, fire suppression has

increased the chance of stand-replacing fires in many remaining old-growth stands. Furthermore, low-elevation habitats undoubtedly support a much smaller proportion of old growth than before European settlement. All seral stages provide critical habitat to some plants and animals (Hansen et al., 1991). Perhaps the best prescription for maintaining biological diversity and sustainable ecosystems is to imitate as closely as possible the natural stand age distribution (Bunnell, 1995). Although the method presented here cannot be used to estimate accurately presettlement stand age distribution, it can help guide managers in protecting adequate amounts of old growth.

ACKNOWLEDGEMENTS

Brian Steele provided helpful discussion and data analysis. Cathy Calloway, Brian Donner, Michelle Dragoo, Ed Lieser and Andy Vigil of Flathead National Forest and Brian Long of the Montana Department of State Lands provided habitat type information and stand maps. Steve Arno, William Baker, Steve Barrett, Anne Bradley, Ed Johnson, Bob Keane and Bruce McCune gave many helpful comments on earlier drafts of this manuscript. Rosalind Yanishevsky gave encouragement throughout the course of the study. Funding was provided by the National Audubon Society.

REFERENCES

Arno, S. F. (1976). The historical role of fire on the Bitterroot National Forest. USDA Research Paper INT-187, Ogden, UT.

Arno, S. F. (1980). Forest fire history in the Northern Rockies. J. For., 78, 460-5.

Arno, S. F. & Davis, D. H. (1980). Fire history of western red cedar/hemlock forests in northern Idaho. In Proceedings of the fire history workshop, Tucson, AZ, USDA Forest Service General Technical Report, RM-81. Fort Collins, CO. pp. 21-6.

Arno, S. F. & Petersen, T. D. (1983). Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. USDA Forest Service Research Paper

INT-301, Ogden, UT.

Arno, S. F. & Sneck, K. M. (1977). A method for determining fire history in coniferous forests of the Mountain West. *USDA Forest Service General Technical Report* INT-42, Ogden, UT.

Baker, W. L. (1989). Effect of scale and spatial heterogeneity on fire-interval distributions. Can. J. For. Res., 19, 700-6.

Barrett, S. W. & Arno, S. F. (1991). Classifying fire regimes and defining their topographic controls in the Selway-Bitterroot Wilderness. Paper presented at the 11th Conference on Fire and Forest Meteorology, Missoula, MT.

Barrett, S. W., Arno, S. F. & Key, C. H. (1991). Fire regimes of western larch lodgepole pine forests in Glacier National Park, Montana. Can. J. For. Res., 21, 1711-20.

Bunnell, F. L. (1995). Forest dwelling vertebrate faunas and natural fire regimes in British Columbia: patterns and implications for conservation. *Conserv. Biol.*, 9, 636-4.

Davis, K. M. (1980). Fire history of a western larch/Douglasfir forest type in northwestern Montana. In *Proceedings of* the fire history workshop, Tucson, AZ. USDA Forest Service General Technical Report, RM-81. Fort Collins, CO, pp. 69-74.

Doak, D. (1989). Spotted owls and old-growth logging in the

Pacific Northwest. Conserv. Biol., 3, 389-96.

Fischer, W. C. & Bradley, A. F. (1987). Fire ecology of western Montana forest habitat types. USDA Forest Service General Technical Report INT-223. Ogden, UT.

Fischer, W. C. & Clayton, B. D. (1983). Fire ecology of Montana forest habitat types east of the Continental Divide. USDA Forest Service General Technical Report INT-141, Ogden, UT.

Franklin, J. F., Cromack, K., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F. & Juday, G. (1981). Ecological characteristics of old growth Douglas-fir forests. USDA Forest Service General Technical Report, PNW-118

Gilpin, M. E. (1988). A comment on Quinn and Hastings: Extinction in subdivided habitats. *Conserv. Biol.*, **2**, 290–2.

Gilpin, M. E. & Soulé, M.E. (1986). Minimum viable populations: Processes of species extinction. In *Conservation biology. The science of scarcity and diversity*, ed. M. E. Soulé. Sinauer Associates, Sunderland, MA, pp. 19-34.

Habeck, J. R. (1983). Impact of fire suppression on forest succession and fuel accumulations in long-fire-interval wilderness habitat types. In *Proceedings-Symposium and* workshop on wilderness fire, technical coordinators, J. E. Lotan, B. M. Kilgore, W. C. Fischer & R. M. Mutch. USDA Forest Service General Technical Report INT-182, Ogden, UT, pp. 110-18.

Habeck, J. R. & Mutch, R. W. (1983). Fire dependent forests in the northern Rocky Mountains. J. Quatern. Res., 3,

408-24.

Hansen, A. J., Spies, T. A., Swanson, F. J. & Ohmann, J. L. (1991). Conserving biodiversity in managed forests. *Bio-Science*, 41, 382-92.

Harris, L. D. (1984). The fragmented forest. University of

Chicago Press, Chicago, IL.

Hart, M. & Lesica, P. (1994). Accuracy of early stand exam age estimates in the Swan Valley of western Montana. USDA Forest Service Research Note INT-422, Ogden, UT.

Hawkes, B. C. (1980). Fire history of Kananaskis Provincial Park-mean fire return intervals. In *Proceedings of the fire* history workshop, Tucson, AZ. USDA Forest Service General Technical Report RM-81, Fort Collins, CO, pp. 42-5

Hejl, S. J. & Wood, R. E. (1991). Bird assemblages in olgrowth and rotation-aged Douglas-fir/ponderosa pinstands in the Northern Rocky Mountains: a preliminary assessment. In *Interior Douglas fir. the species and its management*, ed. D. M. Baumgartner & J. E. Lotan, Department of Natural Resources, University of Idaho, Moscow, ID, pp. 93-100.

Johnson, E. A. (1979). Fire recurrence in the subarctic and its implications for vegetation composition. Can. J. Bot., 57,

1374-9.

Johnson, E. A. (1992). Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge.

Johnson, E. A. & Gutsell, S. L. (1994). Fire frequency models, methods and interpretations. *Adv. Ecol. Res.*, 25, 239-87.

Johnson, E. A. & Larsen, C. P. S. (1991). Climatically induced fire frequency in the southern Canadian Rockies. *Ecology*, 72, 194-201.

Johnson, E. A. & Van Wagner, C. E. (1985). The theory and use of two fire history models. *Can. J. For. Res.*, 15, 214-20.

Lesica, P., McCune, B., Cooper, S. V. & Hong, W. S. (1991). Differences in lichen and bryophyte communities between old growth and managed second-growth forests in the Swan Valley, Montana. *Can. J. Bot.*, **69**, 1745–55.

McClelland, B. R. (1979). The pileated woodpecker in forests of the Northern Rocky Mountains. In *The role of insectivorous birds in forest ecosystems*, ed. J. G. Dickson. Academic Press, New York, pp. 283-99.

McCune, B. (1983). Fire frequency reduced two orders magnitude in the Bitterroot Canyons, Montana. Can For. Res., 13, 121-218.

Morrison, P. H. (1988). Old growth in the Pacific Northwest: a status report. The Wilderness Society, Washington DC.

Norse, E. A. (1990). Ancient forests of the Pacific Northwest. Island Press, Washington DC.

Norse, E. A., Rosenbaum, K. L., Wilcove, D. S., Wilcox, B. A., Romme, W. H., Johnston, D. W. & Stout, M. L. (1986). Conserving biological diversity in our national forests. The Wilderness Society, Washington DC.

Old Growth Definition Task Force (1986). Interim definitions for old-growth Douglas-fir and mixed conifer forests in the Pacific Northwest and California. USDA Forest Service Research Note PNW-447.

Pyne, S. J. (1982). Fire in America—a cultural history of wild-land and rural fire. Princeton University Press, Princeton, NJ.

Rowe, J. S., Spittlehouse, D., Johnson, E. & Jaseniuk, M. (1975). Fire studies in the Upper Mackenzie Valley and adjacent Precambrian uplands. Canadian Department of Indian Affairs, North Devon Arctic Land Use Paper 74-75-61.

USDA Forest Service (1992). Flathead Forest land and resource management plan amendment 16, old-growth MIS standards. USDA Forest Service, Kalispell, MT.

USFS Northern Rocky Mountain Forest and Range Experiment Station (1937-43). Western Montana timber survey. Manuscript 84 Vol. 1-51. Archives, Maureen and Mike Mansfield Library, University of Montana, Missoula.

Van Wagner, C. E. (1977). Conditions for the start and spread of crown fire. Can. J. For. Res., 7, 23-34.

Van Wagner, C. E. (1978). Age-class distributions and forest fire cycle. Can. J. For. Res., 8, 220-7.

Wellner, C. A. (1970). Fire history in the Northern Rocky Mountains. In Role of fire in the Intermountain West: Pro-

ceedings of a symposium; 1970 October 27-29; Missoula, MT. Intermountain Fire Research Council, Missoula, MT, pp. 42-64.

Wilcove, D. S. (1987). From fragmentation to extinction. Natural Areas J., 7, 23-29. Yanishevsky, R. M. (1987). The rise of plans and the fall of old growth. A comparative analysis of old growth in Region One. *Forest Watch*, 7(11), 23-7.

Yarie, J. (1981). Forest fire cycles and life tables: a case study from interior Alaska. Can. J. For. Res., 11, 554-62.